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BIOLOGICAL BULLETIN

THE DEVELOPMENT OF THE CASTES OF NINE GENERA AND THIRTEEN SPECIES OF TERMITES.

CAROLINE BURLING THOMPSON,

DEPARTMENT OF ZOOLOGY, WELLESLEY COLLEGE.

In a former paper (Thompson, 1917), the writer showed that the newly hatched nymphs of the termite *Reticulitermes flavipes* Kol., 1.1 mm. long, although externally all alike, are differentiated by internal structural characters into two distinct types—(*a*) reproductive nymphs and (*b*) worker-soldier nymphs—from which develop (*a*) the three fertile adult castes, the reproductive forms, and (*b*) the two sterile adult castes, the workers and the soldiers. It was further shown that when the reproductive nymphs have attained a length of 1.3–1.4 mm. they are differentiated by internal characters into "nymphs of the first form" and "nymphs of the second form," which develop finally into two of the three adult reproductive castes;[1] at a much later period, when they have attained a length of about 3.75 mm., the worker-soldier nymphs become differentiated by internal characters into the worker and the soldier nymphs.

Bugnion (1912, '13) states that the soldier (nasutus) of *Eutermes lacustris*, a new termite species from Ceylon, is differentiated at the time of hatching, and may be distinguished from the other newly hatched nymphs by both external and internal structures, namely: the frontal process (corne frontale) and the large frontal gland.

These observations of Bugnion are not in accord with the work of Knower (1894) who states that the nasutus of *Eutermes rippertii* (?)—since identified by Mr. N. Banks as *E. pilifrons*

[1] The development of the third, wingless, reproductive caste of *R. flavipes* has not been worked out.

Holmgren—arises late in its development by molting from an antecedent worker-like form with thirteen antennal segments.

In view of these conflicting observations it seemed at first possible that different degrees of differentiation of the newly hatched nymphs, as well as differences in development, might exist in the various genera of termites, and perhaps even among the species of a genus, as, for example, in the genus *Eutermes;* the nasutus of *E. lacustris* being clearly defined at the time of hatching, according to Bugnion; the nasutus of *E. pilifrons* arising rather late in the development by molting from a worker-like form, according to Knower. But, before coming to any conclusion, it seemed desirable to have further data in regard to the conditions among other termites at the time of hatching and in the early stages of development.

The present study of the newly hatched and the developing nymphs of nine genera and thirteen species of American termites, from both temperate and tropical regions, was therefore undertaken for two reasons: first, to ascertain the conditions among different genera of termites, and second, to determine whether the development may vary within a genus, by comparing the conditions in *Eutermes lacustris*, as described by Bugnion, with those of *Eutermes pilifrons*, the Jamaican species observed by Knower, and with two other tropical species, *E. morio* Latreille, and *E. sanchezi* Holmgren.

Material.

Dr. Knower has very kindly sent me an abundance of preserved material of *Eutermes pilifrons*, consisting of eggs, young nymphs, winged adult reproductive forms, and adult workers and nasuti. I am indebted to Mr. N. Banks, of the Museum of Comparative Zoölogy, Cambridge, Mass., for the identification of this species.

Most of my material was furnished me by the Bureau of Entomology of the U. S. Department of Agriculture, and much of it was collected and fixed for me by Mr. T. E. Snyder, to whom my sincere thanks are due. The eggs and young of *Termopsis* I have collected myself at Pacific Grove, Cal., during a visit to the Hopkins Marine Station.

Gilson's fluid has proved a good fixative for the newly hatched nymphs, and Bouin's fluid is excellent for all older forms. As in the case of *Reticulitermes* whole mounts of the newly hatched and developing nymphs, stained with Conklin's picro-hæmatoxylin, are most useful for preliminary study.

The termites to be described in this paper are *Termopsis angusticollis* Walker, *Calotermes* n. sp. Banks, *Cryptotermes cavifrons* Banks, *Neotermes castaneus* Burm., *Arrhinotermes simplex* Hagen, *Reticulitermes flavipes* Kollar, *R. virginicus* Banks, and *R.* n. sp. Banks, *Anoplotermes fumosus* Müller, *Amitermes tubiformans* Buckley, *Eutermes pilifrons* Holmgren, *E. morio* Latreille and *E. sanchezi* Holmgren.

Family.	Genus and Species.	Length, Egg, Mm.	Length, Newly-hatched Nymphs, Mm.	Length, Small and Large Headed Nymphs, Mm.	No. Antennal Segments, Newly Hatched Nymphs.
Protermitidæ ..	*Termopsis angusticollis*....	1.3 –1.7	?	2.8–3	?
	Calotermes n. sp. .	1.2 –1.4	1.6	1.8–2	9, third entire.
	Cryptotermes cavifrons.....	1.2 –1.3	1.4 –1.6	2.4	9, third entire.
	Neotermes castaneus.....	1.6	?	2.6	?, probably 9.
Mesotermitidæ.	*Arrhinotermes simplex*.....	0.8 –1	1.2	2	9, third subdivided.
	Reticulitermes flavipes.....	0.68–0.7	1.1	2	9, third subdivided.
Metatermitidæ.	*Anoplotermes fumosus*.....	0.56–0.6	?	1.8–2	?, probably 11.
	Amitermes tubiformans....	0.56–0.64	0.95–1.0	1.6–1.8	11, third subdivided.
	Eutermes pilifrons	0.64–0.7	0.8 –0.9	1.8–2	11, third subdivided.

In the accompanying table it may be seen that the first four genera belong to the family Protermitidæ of Holmgren, the fourth, together with *Reticulitermes*, belongs to the Mesotermitidæ, and the last three are Metatermitidæ. The present paper therefore includes examples from each family of the order Isoptera.

My study includes for each genus (1) the eggs, (2) the newly hatched nymphs, in some cases these have been actually dis-

sected out from the egg shell, in other cases they are slightly older; (3) an early stage of development, usually 0.2–0.4 mm. longer than the newly hatched nymphs, in which the external appearance, and especially the size of the heads, is similar in all nymphs; (4) a slightly older stage, varying considerably in length in the different genera, in which an external differentiation may be noted in the size of the heads, dividing the developing nymphs into "small headed" (reproductive) forms, and "large headed" (sterile) forms.

Protermitidæ.

Calotermes n. sp. Banks.—The eggs of the most primitive termites, those belonging to the family Protermitidæ, are the largest of the order Isoptera.

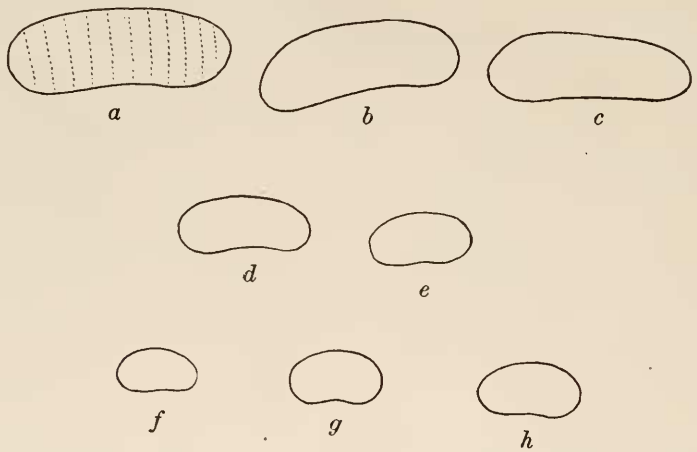

Fig. 1. Termite eggs. *a*, *Termopsis angusticollis; b*, *Calotermes* n. sp.; *c*, *Cryptotermes cavifrons; d*, *Arrhinotermes simplex; e*, *Reticulitermes flavipes; f*, *Anoplotermes fumosus; g*, *Amitermes tubiformans; h*, *Eutermes pilifrons*. Spencer Oc. 6, obj. 32, reduced one third.

The eggs of *Calotermes* n. sp. (Fig. 1, *b*) are long, slender, and reniform, and are slightly larger at one end, the future head end; they measure, in preserved specimens, from 1.2–1.4 mm. in length. In all the species of termites here described the egg length varies several tenths of a millimeter. It would be interesting to know whether these variations in length are constant in the living eggs, and whether they represent two different sizes

of eggs, corresponding to the two different types of nymphs which are hatched. Since this paragraph was written further study of living eggs enables me to state with certainty that there are marked differences in size in the living eggs of a given species and, furthermore, among eggs in the same phases of development.

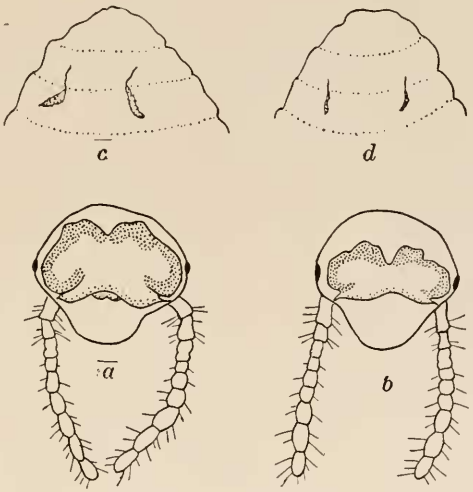

FIG. 2. *Calotermes* n. sp., newly hatched nymphs. *a*, head of reproductive nymph with large brain; *b*, head of soldier nymph with small brain; *c*, testes, reproductive nymph; *d*, testes, soldier nymph. Oc. 6, obj. 16, reduced one third.

The newly hatched nymphs of *Calotermes* n. sp. are 1.6 mm. long, with nine antennal segments, the third segment entire and bare. In size, shape and general external appearance these newly hatched nymphs are all alike, but, as in the genus *Reticulitermes*, they are separable by means of internal structures into two types: (*a*) nymphs with a large brain that almost fills the cavity of the head, large sex organs, and a white dense abdomen, the reproductive or fertile type (Fig. 2, *a*, *c*); and (*b*) nymphs with a smaller brain that does not nearly fill the head cavity, smaller sex organs, and a transparent abdomen, the soldier,[1] or sterile type (Fig. 2, *b*, *d*).

When the *Calotermes* nymphs have attained a body length of 1.8–2 mm. a marked difference in the size of the heads is noted,

[1] The worker caste is lacking in the genus *Calotermes*.

the fertile, or reproductive type having a small head with a larger brain, the "small-headed" nymph of Grassi (1896–97); the sterile, or soldier type, with larger head and smaller brain, the "large-headed" nymph of Grassi. The number of antennal segments in these older nymphs is still nine, although the third segment is deeply grooved and subdivided into two parts. The increase in the number of antennal segments is therefore slightly slower than in the genus *Reticulitermes*, the "small-headed" and "large-headed" nymphs of *Reticulitermes*, 2 mm. in length, having twelve clearly defined antennal segments.

Termopsis angusticollis Walker.—*Termopsis angusticollis* produces the largest egg of any American termite. In form, the eggs are long, slender, and reniform, slightly larger at the future head end, and sometimes with surface markings (Fig. 1, *a*). Both in the living eggs and after fixation, and the eggs shrink very little in Gilson's Fluid, two fairly distinct sizes of eggs may be observed. The smallest are about 1.3 mm. long, the largest range from 1.5–1.7 mm. These size differences are independent of embryonic growth, since a large and a small egg may be in the same phase of development. I am unable to state what types of nymphs may hatch from the different sized eggs, for after searching repeatedly in many colonies in Pacific Grove, Cal., I do not feel sure that I have seen the newly hatched nymphs. The smallest nymphs that I have found are 2.2 and 2.5 mm. long, with eleven and twelve antennal segments. These may be the newly hatched forms, but their size in relation to the egg, their activity, for newly hatched nymphs are usually sluggish, as well as the eleven or twelve antennal segments, inclines me to believe that they have been hatched for a short time. In one embryo with well formed appendages nine segments could be distinguished in the antennae. I am therefore unable to make any definite statement regarding the body length and the number of antennal segments of the newly hatched nymphs of *Termopsis angusticollis*, although from the size of the egg I should expect the nymphs to measure about 1.6–1.9 mm. in length, and the number of antennal segments to be like that of the other Protermitidæ, *Calotermes* and *Cryptotermes*, namely, nine, with the third segment either entire or subdivided.

The youngest nymphs of *T. angusticollis* that I have examined —2.2–2.5 mm. long, with eleven and twelve antennal segments —are all alike in external macroscopic appearance, but with a lens the two types of fertile or reproductive nymphs and sterile or soldier[1] nymphs may be seen. The heads are of similar size, but the large brain almost filling the head cavity of the reproductive nymph (Fig. 3, *a*) is clearly distinguished from the smaller brain of the soldier nymphs (Fig. 3, *b*), and correlated with the brain structure is the whiter denser abdomen of the reproductive nymphs and the more transparent abdomen of the soldier nymphs. In stained and mounted specimens the larger sex organs of the reproductive nymphs are in marked

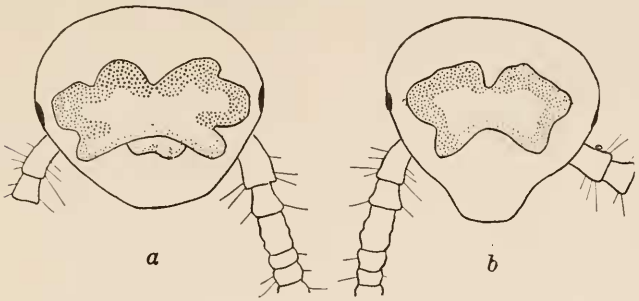

FIG. 3. *Termopsis angusticollis*, young nymphs 1.8 mm. long, with twelve antennal segments. *a*, head of reproductive nymph with large brain; *b*, head of soldier nymph with small brain. Oc. 6, obj. 16, reduced one third.

contrast to the smaller ones of the soldier nymphs. The brain of all the adult castes of *T. angusticollis* has a very characteristic form, as if it had been pulled out laterally, due to the lateral extension of the optic lobes which extend out at right angles to the long axis of the body. This peculiar form of the brain is recognizable even in the youngest nymphs.

Slightly older nymphs of *Termopsis*—2.8–3 mm., with thirteen and fourteen antennal segments—have the heads differentiated in size so that the "small-headed," large-brained, reproductive forms are easily distinguishable from the "large-headed," small-brained, soldier nymphs.

Cryptotermes cavifrons Banks.—The egg of *Cryptotermes*, like

[1] The worker caste is lacking in the genus *Termopsis*.

those of the other Protermitidæ here described, is long slender and reniform, and measures 1.2–1.3 mm. in length (Fig. 1, *c*).

The newly hatched nymphs are 1.4–1.6 mm. long and have nine antennal segments, the third segment entire and bare. These nymphs are externally all alike, but are differentiated internally into the reproductive type with large brain, and large sex organs (Fig. 4, *a*), and the soldier[1] type with smaller brain and smaller sex organs (Fig. 4, *b*).

The peculiar truncated head and the characteristic form of the antennae of this species are recognizable, even in the newly hatched nymphs.

In nymphs which are about 2.4 mm. long the "small-headed" and "large-headed" types are clearly seen. This termite, like

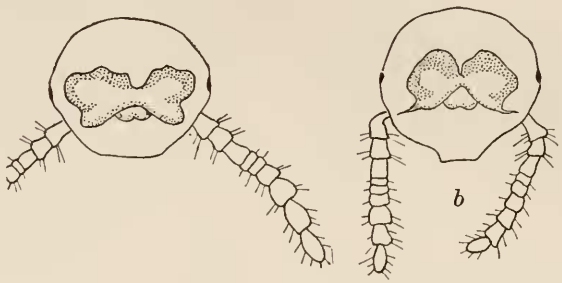

FIG. 4. *Cryptotermes cavifrons*, newly hatched nymphs. *A*, head of reproductive nymph with large brain; *b*, head of soldier nymph with small brain. Oc. 6, obj. 16, reduced one third.

Calotermes n. sp., increases the antennal segments slowly, for nine segments still occur in this older phase, although the third segment is subdivided.

Neotermes castaneus Burmeister.—The egg of *Neotermes*, fig. 5, *c*, is large, measuring 1.6 mm. in length. In form it is slender and reniform like the eggs of other Protermitidae.

The youngest nymphs in my material, which is not very abundant, are 2 mm. long and have ten antennal segments. Since the majority of the termites here described have nine antennal segments when hatched and are only from 0.2–0.3 mm. longer than the egg from which they have emerged, I believe that these nymphs are very slightly past the age of hatching. An examination of the antennae gives further basis for this opinion, fig.

[1] The worker caste is lacking in the genus *Cryptotermes*.

5, *a*, *b*. The fourth antennal segment, which in growing individuals is always the youngest, is short and bears very minute hairs, and in one specimen bears hairs on one side only, indications that this segment has been very recently cut off from the third, probably since the time of hatching.

Externally these young nymphs of *Neotermes* are still all alike, for no differentiation in the size of the heads can be observed, but internally they are differentiated into the two types of nymph

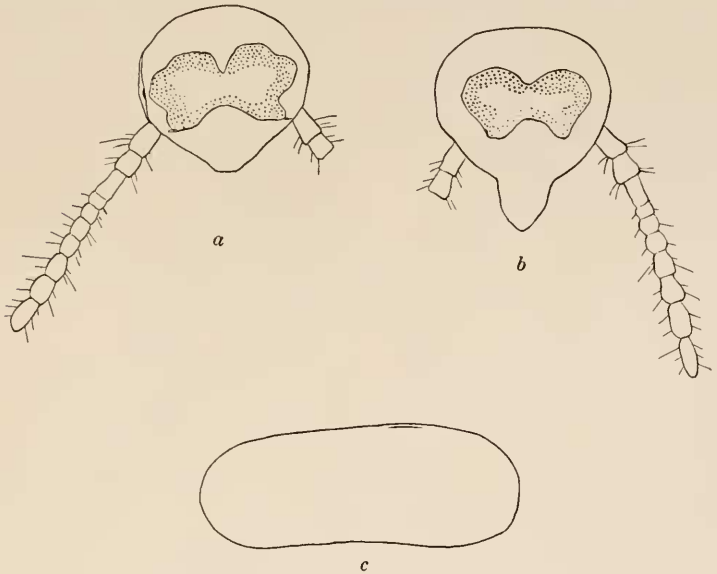

FIG. 5. *Neotermes castaneus*, *a*, head of young reproductive nymph, 1.8 mm. long; *b*, head of young soldier nymph, 1.8 mm. long; *c*, egg. *a*, *b*, Leitz oc. 1, obj. 3; *c*, Leitz oc. 4, obj. 1; reduced one third.

found in the other Protermitidae, namely: the reproductive or fertile type, with large brain, and large sex organs, and the soldier or sterile type, with small brain and small sex organs. The heads of these two types are shown in fig. 5, *a*, *b*.

Nymphs 2.6 mm. in length and with eleven antennal segments have the heads differentiated into the small-headed reproductive type with large brain, and the large-headed soldier type with small brain.

All four genera of Protermitidae are therefore alike in possessing two types of nymphs at the time of hatching.

MESOTERMITIDÆ.

Arrhinotermes simplex Hagen.—The eggs of the Mesotermitidæ are considerably smaller than those of the Protermitidæ. The eggs of *Arrhinotermes simplex* measure from 0.8 to 1 mm. in length and are slender and reniform (Fig. 1, *d*).

The newly hatched nymphs are about 1.2 mm. long, and have nine antennal segments, the third segment grooved and subdivided into two parts.

The two types of nymphs: (*a*) reproductive nymphs, with large brain and large sex organs (Fig. 6, *a*, *c*), and (*b*) worker-soldier

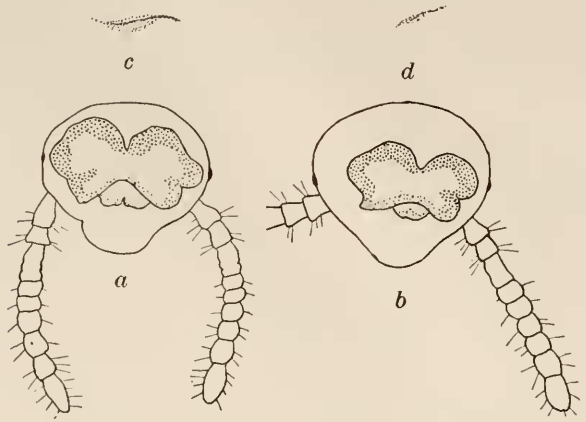

FIG. 6. *Arrhinotermes simplex*, newly hatched nymphs. *a*, head of reproductive nymph; *b*, head of worker-soldier nymph; *c*, ovary of reproductive nymph; *d*, ovary of worker-soldier nymph. Oc. 6, obj. 16, reduced one third.

nymphs, with small brain and small sex organs (Fig. 6, *b*, *d*), are likewise present in this genus at the time of hatching; and with an increase of the body length to 2 mm., the "small-headed" and "large-headed" nymphs are differentiated. There is a striking resemblance between the young of this genus and the related genus *Reticulitermes*.

Reticulitermes.

R. flavipes Kollar.[1] The egg measures from 0.68 to 0.7 mm. (Fig. 1, *e*). The newly hatched nymphs are 1.1 mm. long, with nine antennal segments, the third segment grooved, and are of

[1] For a fuller description of the development of *R. flavipes*, see Thompson (1917).

the two types, reproductive nymphs and worker-soldier nymphs. Nymphs 2 mm. long with twelve antennal segments are differentiated into "small-headed" and "large-headed" types.

R. virginicus Banks.—The newly hatched nymphs of *R. virginicus* are 1 mm. long and have nine antennal segments, the third grooved. They are differentiated into the two types of large-brained reproductive forms and small-brained sterile forms. The further development of this species, so far as I have followed it, is very similar to and probably identical with that of *R. flavipes*.

R. n. sp. Banks.—The young nymphs of a new species of *Reticulitermes* not yet described have been given me by Mr. T. E. Snyder. Examination of this species shows that the conditions at the time of hatching are similar to those in *R. flavipes* and in *R. virginicus*. It seems more than probable therefore that this differentiation of the newly hatched nymphs into two types is common to all species of *Reticulitermes*.

Metatermitidæ.

Anoplotermes fumosus Müller.—The eggs of the Metatermitidæ are smaller than either of the other families of termites. The eggs of *A. fumosus* measure from 0.56 to 0.60 mm. in length (Fig. 1, *f*).

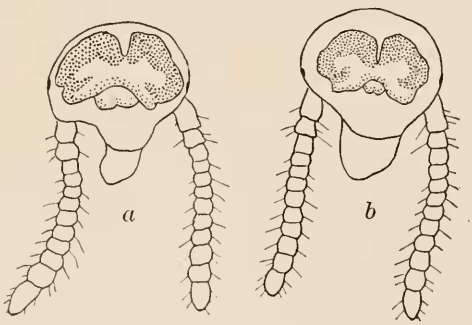

Fig. 7. *Anoplotermes fumosus*, young nymphs 1 mm. long, with twelve antennal segments. *a*, head of reproductive nymph; *b*, head of worker-soldier nymph. Oc. 6, obj. 16, reduced one third.

The youngest specimens of *Anoplotermes fumosus* that I have examined are in an early phase of development, but, on account of their size and the number of antennal segments, I do not think

that they are the newly hatched forms. These specimens measure from 1 to 1.2 mm. in length, and have twelve antennal segments, the third segment being deeply grooved or subdivided. Like the very young nymphs of the other termite genera described above, these young nymphs of *A. fumosus* are externally all alike but are differentiated internally into (*a*) the reproductive nymphs, with large brain and large sex organs (Fig. 7, *a*), and (*b*) the worker-soldier nymphs, with small brain and small sex organs (Fig. 7, *b*). An unusually long slender labrum is present in both types of nymphs, and is characteristic of the three genera of this family here described.

The older nymphs of *A. fumosus*, about 2 mm. long, or less, are differentiated into the "small-headed," large-brained, reproductive type, and the "large-headed," small-brained worker-soldier type. My material was not very abundant, but was sufficient to show that the early development of *A. fumosus* is similar to that of the other termites here described.

Amitermes tubiformans Buckley.—The eggs of *A. tubiformans* measure from 0.56 to 0.64 mm. in length (Fig. 1, *g*).

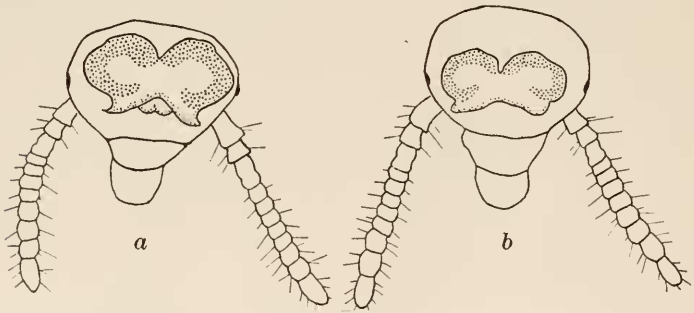

FIG. 8. *Amitermes tubiformans*, newly hatched nymphs. *a*, head of reproductive nymph; *b*, head of worker nymph. Oc. 6, obj. 16, reduced one third.

The youngest nymphs examined are from 0.95 to 1. mm. long, and have antennæ with eleven segments, the third segment bare, but subdivided into two parts. One of these nymphs had a piece of the egg shell still adhering to the abdomen, so that they are evidently the newly hatched forms.

The newly hatched nymphs of *A. tubiformans* are externally all alike, but are differentiated internally into (*a*) reproductive

nymphs with large brain and large sex organs (Fig. 8, *a*), and (*b*) worker[1] nymphs, with small brain and small sex organs (Fig. 8, *b*). The long labrum is prominent in the nymphs of both types.

Nymphs 1.6 –1.8mm. long, with twelve antennal segments, are differentiated into the "small-headed" and "large-headed" types.

Eutermes.

E. morio Latreille.—The eggs of this species of *Eutermes* measure from 0.68 to 0.72 mm. in length and are slender and reniform. The newly hatched nymphs are 1–1.2 mm. long; they have eleven antennal segments, and they consist of the large-brained reproductive type and the small-brained worker-soldier type.

E. sanchezi Holmgren.—I have not seen the eggs of this species but the newly hatched nymphs are very similar to those of *E. morio*. They are 1.2 mm. long, with eleven antennal segments, and the two types of reproductive and worker-soldier nymphs are present.

The newly hatched nymphs of *E. morio* and *E. sanchezi* are almost identical in structure with those of *E. pilifrons* and are therefore not figured; their later development has not been studied, but there is no reason to believe that the three species, which are alike in their early development, should differ in the later phases.

E. pilifrons Holmgren.—The eggs of *E. pilifrons* measure from 0.64 to 0.72 mm., and are slender and reniform (Fig. 1, *h*).

This species was formerly described as *E. rippertii* (?) by Knower, and I am indebted to Dr. Knower for my very abundant material. Many of the nymphs have actually been dissected out from their egg shells, so that there is absolutely no uncertainty as to the structure or the size of the newly hatched forms.

The newly hatched nymphs of *E. pilifrons* measure from 0.8 to 0.9 mm., the difference in length being due to whether the nymphs are still in the curved embryonic position or have straightened out. The number of antennal segments is eleven,

[1] The soldier caste is lacking in the genus *Amitermes*.

with the third segment grooved and subdivided into two parts, so that twelve and thirteen segments will be formed soon after hatching. It is interesting to note the progressive development of the termite order in as small a detail as the number of segments in the antennæ at the time of hatching. The Protermitidæ have nine antennal segments, with the third segment entire; in the intermediate Mesotermitidæ the number is still nine, but the third segment is grooved or subdivided into two parts; in the most highly developed Metatermitidæ the number has increased to eleven, with the third segment subdivided.

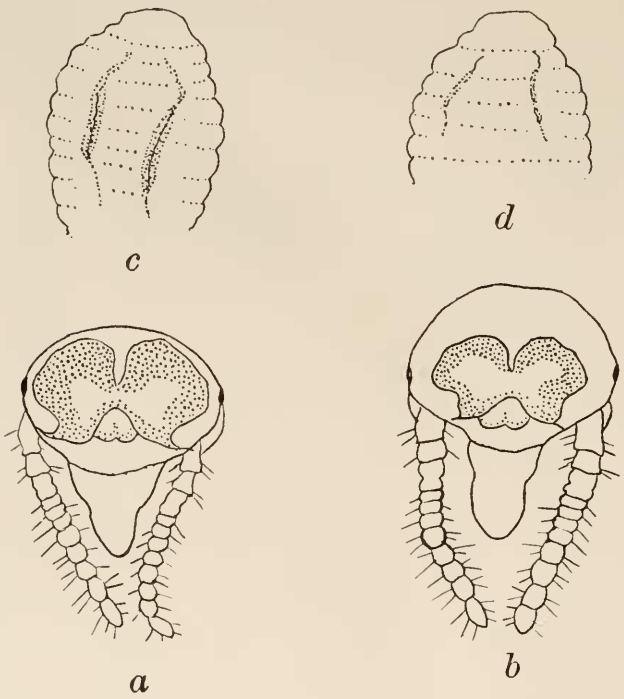

FIG. 9. *Eutermes pilifrons*, newly hatched nymphs. *a*, head of reproductive nymph; *b*, head of worker-soldier nymph; *c*, ovaries of reproductive nymph; *d*, ovaries of worker-soldier nymph. Oc. 6, obj. 16, reduced one third.

E. pilifrons, like all the other termites described in this paper, has the two types of newly hatched nymphs which are alike in external structure:—the reproductive nymphs, with a large brain and large sex organs (Fig. 9, *a*, *c*), and the worker-soldier

nymphs, with a smaller brain and smaller sex organs (Fig. 9, *b*, *d*). The difference between the bodies of fixed specimens of the two types is more marked in this termite than in any other that I have examined; the body of the sterile worker-soldier individuals is a very clear and transparent glistening white, while that of the reproductive individuals is a dull opaque creamy white. A long slender labrum is noticeable in all nymphs of both types.

No appreciable difference in the size of the heads is noted until the nymphs have attained a length of about 2 mm., and have twelve antennal segments. In this phase the "small-headed" reproductive forms with large brain and creamy white body are easily distinguishable with a hand lens from the "large-headed" worker-soldier forms with small brain and transparent glistening white body.

In worker-soldier individuals about 2 mm. long and with twelve antennal segments there is as yet no external differentiation between the two sterile castes, but an internal differentiation has already begun and may be observed in whole mounts of stained individuals as well as in sections. The future soldiers are distinguishable by the presence of the larger frontal gland which appears, in frontal mounts of the head, as a small dense spot posterior to the brain; in whole mounts of the head of the future worker no such spot is visible. After examining the stained specimens in cedar oil to separate the future soldiers from the future workers, the two kinds of individuals were embedded and sectioned. In the soldier nymphs a large, although embryonic, frontal gland opens to the exterior on the frontal surface of the head. This gland was more than three times the size of the vestigial gland found in the worker nymphs.

The soldier caste of *E. pilifrons* is, therefore, not differentiated by external characters at the time of hatching, but arises later in the development, being first manifested in individuals about 2 mm. long with twelve antennal segments. The worker caste is differentiated at the same time, and the two castes may be recognized by the size and structure of the respective frontal glands; although no external differentiations are yet present in either caste.

The differentiation of the worker-soldier nymphs of *E. pilifrons* into the worker and the soldier is nearly parallel with the development of these two castes from the worker-soldier form in the genus *Reticulitermes*, Thompson (1917, pp. 123–125); the chief difference being the age of the respective nymphs, the differentiation being visible in *E. pilifrons* in nymphs 2 mm. long, while in *R. flavipes* it was first observed in nymphs 3.75 mm. long, although, from the maturity of the frontal gland, it could probably be seen in an earlier phase.

My work upon this species of *Eutermes* is in perfect accord with the work of Knower (1894), who noted the absence of young soldier nymphs in the colonies of *E. rippertii* (?) = *E. pilifrons* Holm., and who later saw a young soldier of this species emerge by molting from a worker-like skin. The mandibles on the skin were large, as in *Eutermes* workers, while those of the emerging soldier (nasutus) were small, like those of the adult nasuti. The head of this nasutus was light in color and not yet fully elongated.[1]

Bugnion (1912) states that the soldier (nasutus) of *E. lacustris* is differentiated at the time of its emergence from the egg, and is distinguished from the other newly hatched nymphs by a long frontal process or horn, and a frontal gland with an excretory canal. His description is as follows:

"Larve de soldat, longue de 1.32 mm, venant d'éclore (Fig. 12). Cette forme est particulièrement intéressante parce qu'elle montre une petite corne implantée au dessus du front. Elle donne ainsi la preuve que la caste 'soldat' se différencie déjà dans l'oeuf. La corne, tres courte, ne dépasse pas le niveau des pièces buccales. On voit aussi, par transparence, l'ampoule céphalique entourée de muscles et, à la base de la corne, le canal excréteur."

Now, although I am fully in accord with the view of Bugnion that the castes of termites are not produced by food or other external influences, and that they are due to intrinsic deep-

[1] Snyder (1915) has also described the origin of a soldier nymph from a worker-like form in *Reticulitermes flavipes* and *R. virginicus*. The nymphs were found in the quiescent stage that precedes a molt, and the emergence of the young soldiers was observed. In this case, too, the mandibles of the emerging form differed from those on the cast skin.

seated causes, I am inclined to believe, for several reasons which follow, that Bugnion's account of the newly hatched soldier (nasutus) nymph of *E. lacustris* may be capable of a different interpretation.

First, the conditions among the newly hatched and the younger developing phases of the nine termite genera here described are practically similar, showing that throughout the entire order of termites the early development is remarkably constant.

Second, I have examined the newly hatched and the developing nymphs of three species of *Reticulitermes*—*R. flavipes*, *R. virginicus* and *R.* n. sp.—and also of three species of *Eutermes*—*E. pilifrons*, *E. morio* and *E. sanchezi*—and in each case the development of the three species is similar throughout the early phases and as far as I have followed it. It seems probable, therefore, that *E. lacustris* would follow the plan of development that is common not only to three other species of its genus and to three species of *Reticulitermes*, but to seven other genera.

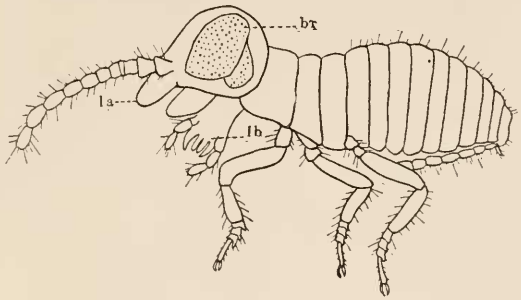

FIG. 10. *Eutermes pilifrons*, newly hatched nymph, profile view. *la*, labrum; *lb*, labium; *br*, brain. Oc. 6, obj. 16, reduced one half.

Third, in all the newly hatched nymphs of *Eutermes*, whether *pilifrons*, *morio* or *sanchezi*, the labrum, as stated above, is long slender and conspicuous. In nymphs seen in profile the side view of this labrum is surprisingly like the frontal process or "corne frontale" of a nasutus. In studying the younger *Eutermes* nymphs in alcohol I remarked again and again the length of the labrum and its resemblance, especially in profile view, to the frontal process of a nasutus. This is also true of the other two genera of the Metatermitidæ here described, *Anoplotermes* and *Amitermes*.

In my Fig. 10, the profile view of a recently hatched *worker-soldier* nymph of *E. pilifrons*, the resemblance is very striking to Bugnion's figure 12 (1912), the profile view of the form which Bugnion has described as a newly hatched *soldier* nymph of *E. lacustris*. The long labrum, *la*, might have been taken for the "corne frontale," the dark stippled mass, *br*, which represents the brain as seen through the transparent skin of the head, might easily be mistaken for the frontal gland that is shown in Bugnion's figure in about the same position. The duct of the frontal gland figured by Bugnion might prove to be the esophagus, which passes forward as a slender tube beneath the brain. Furthermore, the frontal gland as figured by Bugnion in the newly hatched soldier (nasutus) of *E. lacustris* is much larger and more highly developed than in the older nymphs of *E. pilifrons* 2 mm. long, and is also larger and more developed than I have found it in any newly hatched termite nymphs that I have studied. As a rule this gland is not distinguishable at the time of hatching except in sections, and even then is extremely small and difficult to determine.

Fourth, Professor Bugnion's figure was drawn from an unstained specimen, mounted, as he states, in either water or weak formol, and studied as a transparent object. If after staining and sectioning the same results are obtained in the newly hatched nymphs of *E. lacustris* we should then have positive proof that development varies in the different species of a termite genus and that some castes may be fully differentiated at the time of hatching. But, until this proof is established, the writer is inclined to believe that development is a constant process among the different species of termites, and that it takes place as in the termites here described.

Summary.

The termites described in this paper are:

Protermitidæ—

Termopsis angusticollis.
Calotermes n. sp.
Cryptotermes cavifrons.
Neotermes castaneus.

MESOTERMITIDÆ—

Arrhinotermes simplex.
Reticulitermes flavipes.
" *virginicus.*
" n. sp.

METATERMITIDÆ—

Anoplotermes fumosus.
Amitermes tubiformans.
Eutermes morio.
" *sanchezi*
" *pilifrons.*

1. The eggs of these termites are largest in the primitive forms, the Protermitidæ, measuring from 1.2 to 1.7 mm. in length, they are smaller in the Mesotermitidæ, from 0.68 to 1 mm. long; and are smallest in the Metatermitidæ, from 0.56 to 0.72 mm. long.

2. The newly hatched nymphs correspond in size to the eggs from which they have hatched.

3. The newly hatched nymphs are externally all alike, but they are differentiated by internal structural characters into *two* clearly defined types: (*a*) the *reproductive*, or *fertile forms*, with large brain and large sex organs, and usually a dense opaque body; and (*b*) the *worker-soldier*, or *sterile forms*, with small brain and small sex organs, and usually a clear transparent body.

4. At the time of hatching the antennæ of the Protermitidæ (*Calotermes* n. sp., *Cryptotermes cavifrons*, and probably also *Termopsis angusticollis* and *Neotermes castaneus*) have nine segments, with the third segment entire; those of the Mesotermitidæ (*Arrhinotermes simplex*, *Reticulitermes flavipes*, *R. virginicus* and *R.*, n. sp.) have nine segments with the third subdivided; those of the Metatermitidæ (*Amitermes tubiformans*, *Eutermes pilifrons*, *E. morio* and *E. sanchezi*, and probably also *Anoplotermes fumosus*) have eleven segments, the third subdivided.

5. Nymphs with a body length of about 2 mm., or 2.5 to 3 mm. in the larger genera, are differentiated into "small-headed" but large brained reproductive forms, and "large-headed" but small-brained worker-soldier forms.

6. The worker-soldier nymphs of *Eutermes pilifrons*, 2 mm.

long, with twelve antennal segments, and externally all alike, are distinguishable, after staining, into worker nymphs with a small vestigial frontal gland, and soldier nymphs with a large frontal gland.

7. The soldiers of *Eutermes pilifrons*, and also those of *E. morio* and *E. sanchezi*, are therefore not externally differentiated at the time of hatching, which, according to Bugnion, is the case in *E. lacustris*.

Wellesley, Mass.,
July, 1918.

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